Biological studies on *Bradyporus multituberculatus* F. W.
(Orth., Tettig.)

BY

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(Lámina I.)

I. Taxonomy, synonymy and distribution of the species.

Representatives of the peculiar circum-Pontic genus *Bradyporus* Charp. have been recorded by various authors under different, often undoubtedly incorrect, names from the following provinces of Russia in Europe: Bessarabia, Kherson, Tauria, Ekaterinoslav, Kharkov, Voronezh, Black Sea (Tchernomorskaya), Stavropol, Don, Kuban, Terek, as well as from the Transcaucasia.

Most of the records refer to the genus as *Callimenus*, but I accept the opinion expressed by Uvarov (1923, p. 154) that *Callimenus* Burm. (= *Deralimmus* Caud.) cannot be separated from *Bradyporus* Charp. (= *Dinarchus* St.) and the latter name has the priority.

Species of the genus *Bradyporus* are remarkable for their great geographical and individual variability, and describing of new species, particularly on a small number of specimens, often led, apparently, to serious mistakes. A thorough revision of the genus is, therefore, urgently needed, and the character most suitable for separating the species seems to be the structure of the male cerci (such a revision is contemplated by the author jointly with B. P. Uvarov).

As regards the species occuring in the European Russia, I had the opportunity to study specimens of *Bradyporus* from the Don province and Northern Caucasus, where this insect still occurs in fairly large numbers in the virgin steppes, with which the insect is connected ecologically; they are, for instance, fairly common in the steppes along the middle course of the river Kuma, and, especially on the middle Terek, between the mouth of Malka and Sunzha (Terek province).

I actually examined, specimens from the vicinity of Novotcherkassk, from the shores of the Azove Sea, from the Taman peninsula, vicinity of Novorossiisk, from various places in the Kuban and Stavropol province. For comparison I have studied also specimens of *Bradyporus* (in the Zoological Museum of the Russian Academy of Sciences) from Rumania (and Dobrudzha), Yugo-Slavia, Greece, Syria and Asia Minor.

After comparing all studied materials I arrived to the conclusion, that in the Don province and Northern Caucasus occurs only one species, with very definite characters, and well distinct from the Anatolian and Balkanian species, though very near to the Rumanian *B. montandoni* Burr, a cotype of which I have also studied.

This North-Caucasian species was best described by Shugurov (1906) under the name *Callimenus brauneri* Shug., but it has an earlier name—*Bradyporus multituberculatus* F. W. (1833); a still earlier name, by the same author (1830) canott be acepted, being a *nomen nudum*.

The synonymy of the species in question is, as follows:

1830. *Callimenus obesus*, Fischer Waldheim (*nomen nudum*).

1833. *Bradyporus multituberculatus*, Fischer Waldheim.

1846. *Bradyporus oniscus*, Fischer Waldheim.

1905. *Callimenus restrictus* (nec F. W.), Shugurov (also Shugurov, 1906).

1906. *Callimenus brauneri*, Shugurov (also Uvarov, 1915; Boldyrev, 1915).

I am very much obliged to Mr. B. P. Uvarov for the friendly help in establishing the synonymy, as well as for the assistance in the work generally and for the translation of the paper from Russian manuscript.

II. **Ecology and annual life cycle.**

There is nothing in literature on biology of *B. multituberculatus*, apart from few general notes (Boldyrev, 1915, p. 107); neither is the biology of other species known, though recently some information has been published with regard to *B. dasypus* Ill. and *B. pancici* Br. W. by Burr (1916, 1916 a), Campbell (1923) and Georgevitch (1926).

My observations on *B. multituberculatus* covered only a short

period (from 28th July to 28th August 1917), which also partly coincided with the seasonal decline in the activities of the insect, but I still think it worth while to publish the data obtained, because the species seems to be dying out in Russia, in connection with the decrease of the virgin steppes, as it was pointed out by Uvarov (1915, p. 93). In some parts of its area, *B. multituberculatus* already became a great rarity, or disappeared altogether, under the influence of culture; this happened, for instance in the Voronezh province and in the Ukraine (see the last chapter).

My observations were conducted in the environs of the station Prokhladnaya (on the river Malka, a tributary of Terek), on the estate of the Agricultural School. The estate was practically all under cultivation, but there were some patches of virgin steppe with typical shrubs, as well as some areas, which were left without cultivation for 12 years.

At the end of July the vegetation, owing to a month of drought, was burnt by sun and this process continued throughout the August. Most of all burnt were the places uncultivated for 12 years, were the only green plants on the yellowish-grey background where the scattered shrubs of *Rhamnus pallasii* F. et Mey., *Prunus spinosa* L., small clumps of *Glycyrrhiza glabra* L., *Artemisia campestris* L., *Salsola kali* L. and *Teucrium polium* L. In places the steppe was whitish grey from *Artemisia austriaca* Jacq., and the entirely dried up, brownish shrubs of *Achillea nobilis* L. were densely covered by the white shells of the mollusc *Xerophylla* sp., which patiently waited for the rain. Of the grasses, only groups of *Stipa capillata* L., and of *Bromus squarrosus* L. were to be seen, while *Cynodon dactylon* Pers. occured near the roads. Some variety in the monotonous landscape of the burnt steppe was introduced only by the whitish-pink groups of *Xeranthemum annuum* L. and by some still flowering plants of *Althaea ficifolia* Gav., *Centaurea solstitialis* L., *Marubium praecox* Janca and *Delphinium consolida* L.

The areas of the virgin steppe, owing to their less elevated position (in the valley of the river Malka) were less burnt. Here the shrub vegetation predominated, either in the shape of a dense growth, or in small scattered groups, *Rhamnus pallasii*—the favourite plant of *Bradyporus*—being particularly numerous, while *Prunus spinosa* was also

common, and *Ligustrum*, *Berberis* and *Rosa* occurend, as well. The open spaces between the groups of shrubs were covered by grasses (often by *Stipa capillata*) and by *Glycyrrhiza glabra;* amongst the partly burnt grasses some flowering plants were present, like *Statice gmelini* Willd., *Centaurea solstitialis* L., *Nigella arvensis* L., *Eryngium campestre* L., *Delphinium consolida* L., *Aster* sp. and *Cephalaria* sp.

On the cultivated fields in August millet, maize and sunflower were still standing, while oats and mustard were cut, but not yet taken away from the fields.

Soils in the vicinity of the station Prokhladnaya may be classed as middle light loamy black solis (tchernosem), slightly alkaline.

Amongst the climatic characteristics of the region influencing the seasonal changes in the vegetation, the droughts continuing for nearly 3,5 months (from the end of July to October) must be specially mentioned; owing to them, the vegetation, which develops luxuriously from beginning of April to the second half of June, is then quickly burnt. The winter months (December, January, February) are characterised by the presence (from January) of a snow cover and by the frosts, reaching sometimes —20-25° C.

Bradyporus was fairly common in the environs of Prokhladnaya, though according to the evidence of local peasants, this insect varies in numbers from year to year. In 26 days of my sejourn there I have collected 54 males and 4 females, sometimes taking more than ten specimens during a single excursion (on the 29th of June 11 males and one female were taken in half an hour; on the 2nd August-13 males in an hour). Most often I found the insects on an area of virgin steppe, densely covered with shrubs, mainly *Rhamnus pallasii;* fairly common they were also on the long uncultivated soil, where they occured near the scattered shrubs and groups of grasses with thick stems. Finally, *Bradyporus* occured also on the uncultivated strips between fields and on the fields themselves, where they apparently wander from the adjoining virgin or uncultivated areas, because I never found them penetrating very deep into cultivated fields.

As I was told by the peasants, *Bradyporus* is fairly common also in the fields occupied by wheat, where the insect are very noticeable after the wheat is cut; a good many of the insects are carried with the sheafs to the threshing grounds, where they are killed during the operation.

The close connection of *Bradyporus* with uncultivated soils was already pointed out by several authors (Uvarov, 1915; Shugurov), and my observations confirmed it.

Judging by the dates of specimens in the collections and by the information communicated by several entomologists to me (B. P. Uvarov, V. V. Modestov, E. V. Jatsentkovsky), the annual life-cycle of *Bradyporus* must be, as follows. April and May are passed in the larval stage, amongst the green spring vegetation; first adults begin to appear early in June, and soon the songs of the males and the copulation begin; in July the eggs are laid and this is continued into August, when the insects gradually become weaker and die. The eggs hibernate in the soil (regarding the possibility of a diapause in the egg stage see below).

Apart from observations on *Bradyporus* in the field, during excursions undertaken at different times of the day, I kept the insects also in captivity, in a special empty room, with a window on the southern side which was always kept open. On the floor were placed bushes of *Rhamnus pallasii*, bundles of *Glycyrrhiza*, *Setaria* and millet, as well as various vegetable and animal food. As many as 15-25 specimens of *Bradyporus* used to be kept at a time and they seemed quite contented crawling about the floor, sometimes climbing the plants, or hiding in them.

Some individuals, one to three at a time, were placed also for special observations into small wooden cages with metallic wiring.

All my captives were very indifferent to my presence in the room and continued their songs, feeding and courting, not even exhibiting any excitement, when I took them into my hands.

III. **Food and feeding habits.**

The excreta of *Bradyporus* are very large and peculiar in shape (fig. 1) [1]. They are 12-20 mm. long and 3-4 mm. in the diameter; elongate-cylindrical, more or less bent at the ends, which are either

[1] All illustrations for this paper are made under my supervision, and partly from my preliminary sketches, by M-lle A. A. Bayukova, to whom I am very much obliged for her most carefully executed work.

rounded, or, more seldom, attenuated into a pointed short appendix; their surface is often covered by shallow transverse folds; the colour blackish, brown, or greyish-green, sometimes with paler spots on a dark background. When the fresh excreta are rubbed they crumble into green porous mass consisting mainly of vegetable matter. A detailed microscopical analysis of both the excreta and the stomach contents of *Bradyporus*, enabled me to see that its food is 99 per cent vegetable, while only not more than one per cent is of animal origin, this being remains of chitinous parts of insects (elytra, mandibles, legs, apparently, of Coleoptera). Amongs the vegetable matter, which is ground by the mandibles very evenly, but coarsely, were found bits of leaves, parts of hard stems (2-3,5 mm. long), seed-covers, vegetable hairs, etc.

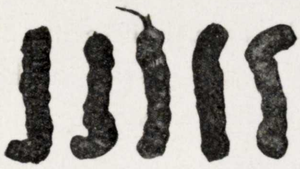

Fig. 1.—Excreta of *B. multituberculatus;* nat. size.

In captivity the insects ate readily the juicy pulp of water-melons, white bread, leaves and unripe seeds of millet, leaves of maize, leaves and berries of *Rhamnus pallasii* (often rejecting the seeds), slightly wilted leaves of roses; they liked less the cucumbers, leaves of beetroot and *Setaria italica*. White bread they ate with a particular greediness and the insects devoured it even when kept in the hand by pronotum. Very readily they ate also freshly killed Acrididae and Tettigoniidae, as well as the bodies of their own comrades, which died, or perhaps, were almost dying from senility. Both sexes were, generally, very peaceful and did not attack each other even when kept in very small cages. The greediness and haste, with which *Bradyporus* eats freshly killed insects are astonishing; various parts are devoured without any choice, so that, for instance, elytra of an Acridid may be devoured, while the abdomen is left. When eating an insect, *Bradyporus* opens its mandibles widely and nods its head rythmically, showing the reddish-brown membrane of the neck; the legs of the front pair often support the insect which is devoured. The appetite of *Bradyporus* is rather large: in one case a male ate two adult *Oedipoda* at one meal.

In its tendency to take under artificial conditions both animal and vegetable food *Bradyporus* does not differ from the majority of *Tettigoniidae*, but in the nature it is undoubtedly mainly vegetarian, which

is accounted for by its clumsiness preventing it to hunt more quickly moving insects. The very insignificant percentage of animal remains (bits of chitin), which can be revealed by the analysis of the stomach contents, must be apparently entirely due to the accidentally found bodies of dead insects, or very slowly moving species.

Water is taken by *Bradyporus* very readily and when I sprayed the plants and the floor in a cage, they crawled to the drops of water and drunk them, stretching their necks and moving the palpi.

IV. **Behaviour in the nature and in captivity; daily regime; songs.**

Bradyporus is a very clumsy and heavy insect, entirely incapable to jump, while it crawls very slowly, somewhat dragging its abdomen and swinging about; seldom its crawling is replaced by a resemblance to a run (when frightened). If a *Bradyporus* falls on its back, it is only with great difficulties that it can regain its legs again. A *Bradyporus*, when sitting on a plant, usually tries to rest its abdomen, or sternum, on a forked branch; legs are partly resting on the plant, but some of them may be dangling in the air; the whole posture is very characteristic for its laziness and clumsiness (Plate I, fig. 1). One can approach a sitting *Bradyporus* very closely and it still remains in its place, or begins to drop very clumsily from one branch to another, until it reaches the ground, where it either remains at the base of the plant, or slowly crawls deeper into bushes.

When a *Bradyporus* is taken by fingers at the sides of the pronotum, it often ejects blood from the special slits (see below, chapter V), with its abdomen hanging heavily and forming a distinct angle with the thorax, and the legs dangling helplessly in the air. Sometimes, however especially the strong, not very old adults, attempt to push away from the hand by their legs, but I have never seen a *Bradyporus* to use its strong mandibles in self-defence.

Often, when taken in hand, *Bradyporus* emits from its mouth a limpid, seldom brownish, drop up to 4,5 mm. in diameter, which remains usually on the mouth parts, and more seldom drops to the

ground. Sometimes, the insects, when frightened, dropped excrements, as well.

When to a *Bradyporus* sitting on the ground a finger is approached now from one side, then from the other, the insect quickly turns away from it, somewhat rising on its legs at the same time.

The stridulating apparatus (vena stridens) placed on the abbreviated reddish-brown, cup-shaped elytra, is developed in both sexes, but in the females the sound produced is less loud, interrupted, and is emitted, apparently, only in fright and in response to the calls of males. The males have great powers of producing sound and can sing nearly whole days throughout; even weak old individuals can produce hoarse, interrupted creaking songs. The song of a healthy and strong *Bradyporus* can be heard in a still evening at the distance of 140-170 metres; it is a continuous trill, in which crackling is mixed with a metallic rustling sound- r′r′z′sch′... When one entered my room with a chorus of the insects the ears begun to tingle and it seemed that one was in a workshop, where drilling of metal was in full progress.

A *Bradyporus* sitting on the ground, when beginning to stridulate, slighly rises its thorax on the first two pairs of legs, while the abdomen is lowered until it touches the ground; hind part of the pronotum is raised and the rapidly vibrating elytra are visible under it. A singing male breathes very rapiddly and deeply, the abdomen pulsating and the anterior part of the body nodding. Singing can be continued during a meal, and the males resume their song immediately after copulation.

In the field, the males (unless they are very old and feeble) for singing climb the plants, but not higher than 1,25 metre and sit there in the lazy and comfortable posture presented in the fig. 1 (Plate I).

Both sexes are capable, when frightened (at capture) to produce a short sound, like «tch'tsk».

My captives began their songs usually after midday (from 2-3 p. m.), at first emitting short trills, but about 5 or 6 p. m. a general deafening chorus was formed and continued all night, no matter whether it was dark, or there was a moon. The songs began to cease in the small hours of the morning (about 3,5-4 a. m.), and towards 7-8 an almost complete silence reigned until the afternoon. During this interval the insects were less active; the females often hid themselves in grass or

shrubs, while the males sat warming themselves in the sunshine, and only seldom emitting short trills. Activities, i. e., crawling from one place to another, climbing the plants, courting, singing began only in the afternoon.

In cloudy or rainy days the songs of captive males begun earlier (after one o'clock), and stopped in the morning later (about ten). Before a thunderstorm, or during a rain with storm, the insects stopped or interrupted their songs even in the evenings, both in the field, and in the room. In the field I never heard the song of males during the mornings, or at midday and early hot afternoons; they started singing when the heat became less intense from 5-5.45 on hot days, and from 4.15-4.30 on cloudy days. First trills were short, but within half an hour a chorus was formed, which was heard in the steppe until late in the night. In warm nights, I believe, the males sing until the morning, but I was unable to prove it, night excursions in the steppe being not safe. Some males, taken into open in a cage continued to sing until 10 o'clock in complete darkness, in spite of rainy weather.

The daily behaviour of the insects, particularly in the field, is undoubtedly governed mainly by the temperature factor, which is especially clearly demonstrated during the hot second half of summer. Observations in captivity proved conclusively that *Bradyporus* cannot stand strong direct sunlight. When the cages with the insects, or single insects, were taken at midday and placed on the groung under direct rays of sun, they begun to breath rapidly and heavily and tried to hide themselves under some shelter. At midday the floor of the room, where the insects were kept, was in places strongly warmed by the sun, and the insects segregated there, but always sat just round these spots, only in exceptional cases entering the area directly warmed by the sun.

In the field I also never found *Bradyporus* sitting openly or crawling about at day time or in the mornings; they are then all hidden amongst grass or shrubs, or, perhaps, also in the empty burrows of small steppe rodents, which were fairly common in the same places. During that hot time of the day steppe was made alive by the songs of *Gampsocleis glabra*, *Decticus verrucivorus* and *albifrons*, *Metrioptera bicolor* and various *Acrididae;* only when the heat abated, *Bradyporus* appeared from their shelters and begun their trills.

It is not impossible that earlier in the season (May, early June) when it is less hot and more shelter is offered by the fresh vegetation, the daily regime of *Bradyporus* differs somewhat from that observed by me in August, during a drought and in a completely burnt steppe.

The favourite haunts of *Bradyporus* in the steppe are the bushes of *Rhamnus pallasii*, round the base of which dense grass grows; these offer very suitable shelter for the day time, while the males climb the bushes for their singing. Apart from *Rhamnus*, the males climb for this purpose also some other sufficiently strongs plants, like *Glycyrrhiza glabra*, *Salsola kali*, *Artemisia campestris* or even dense clumps of grasses, like *Cynodon dactylon;* on cultivated fields, they climbed piles of cut plants.

The males always sat singly, 8-15-140 and even more metres from each other. It may be remarked, that the insects, with their large bronze-black body with yellowish spots on the abdomen, were extremely easy to see even from afar. When a singing male is, moreover, sitting with the sun on the side opposite to the observer, two translucent reddish spots are visible in the hind parts of the lateral lobes of the pronotum, this being the color of the lobes on the inside.

When catching the insects, I approached a singing male and it ceased its song sometimes when I was 3-4 metres from it, but usually it continued until one approached it quite closely, and only my outstretched hand made it to emit a frightened «tch'tsk» and become silent. I have already described above the behaviour of a frightened *Bradyporus*, which is remarkable for the complete indifference of the insect to danger. Sometimes, after taking a male from the bush, I put it on the ground and it remained there, not attempting to get away. In one case, a male taken from a bush and emitting some blood (autohaemorrhage, see next chapter) was put on the bush again and after 10 minutes it was singing again. My captives begun their merry songs very soon after the capture, sitting in the small cage which I took on excursions, or even in the entomological net, where there might be several of them together.

The females were very scarce (only four were found to 54 males), but this is, probably, due to their more concealed and silent habits, which makes finding them much more difficult than the males.

In all cases the females were found near a male. Twice I have

found a female sitting under the bush, on which a male was singing, about half a metre distance from him. Once I saw a female, which, with short shrieks crawled to the base of a *Rhamnus*-bush, on which a male was singing. One female was even taken when she came from the grass to a cage with a male, just captured and singing. This proves beyond doubt, that the females are attracted by the songs of males. This fact was already observed by Steven, who found these insects in the Taman peninsula «toujours par paires» (Fischer Waldheim, 1846, p. 219).

Throughout August I used to find, side by side with fresh and vigorous individuals, also some which exhibited characters of old age. In the males it was noticeable in the song, which became more hoarse and interrupted. In the old individuals of both sexes claws on the legs, tarsi and even tibiae were often lost; antennae were half broken, abdomen shrunk on the pleurites. The insects became feeble, their ability for the autohaemorrhage lessened, they could crawl with difficulty, owing to the febleness of legs, which did not bent well in the joints; excreta became smaller. Still, all these invalidity, did not influence the sexual instincts of the males, which continued to sing and even attempted to copulate; one old male even produced a spermatophor (see chapter VI).

The lenght of the adult life of an individual seems to be considerable, extending at least over 2,5-3 months. Thus, a female captured on the 8th ot June 1924 lived in captivity (at the Plant Protection Station in Essentuki) until the 12th of August, having been fed mainly on various fruits. Males, collected in June 1913 were kept in captivity and fed on fruit (apples, pears), without the females, until the end of August (Boldyrev, 1915, p. 107).

V. **Autohaemorrhage and its meaning.**

The very first *Bradyporus*, which I have captured, demonstrated to me its curious ability to exude a great amount of yellowish fluid (blood, haemolymph) from the special pores on the thorax and abdomen.

This peculiarity of *Bradyporus* was first recorded by Lefebvre

(1831) who observed in June 1829 in the environs of Smyrna a species of *Bradyporus*, which he called *Ephippiger macrogaster* Lef. He described it, as follows: «Lorsqu'on saisit cet insecte, il laisse échapper des bords postérieurs du corselet une liqueur épaisse, d'un jaune gomme-gutte, abondante, d'odeur fétide et légèrement âcre.»

Brunner v. Wattenwyl (1882, p. 251) mistakenly assumed that the liquid comes from the membrane between the first and second abdominal tergites: «Dieses Genus besitzt die Eigentümlichkeit, das es bei Annäherung aus den Zwischenräumen des ersten und zweiten Dorsalsegments des Hinterleibes einen gelben Saft in grossen Tropfen ausschwitzt.» This description provoked some doubts in Vosseler's mind (1902, 1903), who was inclined to think that the liquid is exuded from the longitudinal folds provided with slits (Blutungsspalte) on the back of the upper surface of the pronotum. These interpretations of Brunner and Vosseler were repeated without comment by Hollande in his papers on the haemorrhage in insects (1911, 1911*a*).

M. Burr who observed the Balkanian *B. dasypus* Ill. described the phenomenon more definitely: «The defensive yellow fluid mentioned above is ejected from the longitudinal folds which are situated on the metazona of the pronotum and on the tergites; the fluid is thrown to a distance of four of five inches (1916, p. 145-146; also Doflein, 1921, pp. 83-84).

These are all the literature data on the phenomenon of ejection of blood by *Bradyporus* and an exact description of the process, as well as its explanation, are still wanting. The phenomenon generally was given by Hollande (l. c.) the name of autohaemorrhage, with the following definition: «Je désigne l'émission du sang chez les Insectes du nom de «autohémorrhée» voulant spécifier ainsi l'émission de son sang par l'Insecte lui-même.»

I had the opportunity to study closely the external mechanism of the ejection of blood in *B. multituberculatus*, but with regard to the elucidation of the biological meaning of the process, I had to leave open a number of questions.

In literature on this species the haemorrhage has been recorded by me (1915, p. 107) from what I was told by others, but incorrectly, as it proved to be; I stated then, that the fluid is emitted by frightened insect from under the elytra. In a later paper (1920, p. 28) I descri-

bed it more correctly, saying, that this species has «an ability of the autohaemorrhage, or throwing out the blood with defensive purposes, from the coelomopores of the tergites of the thorax and abdomen». This habit of the insect proved to be known also to peasants of the Terek province, who call it «oily», i. e., emitting a fluid similar to a vegetable oil; in some other places in the North Caucasus *Bradyporus* is also called «fatty cricket».

According to my observations, the emission of blood in *B. multituberculatus* occurs on the tergites of the prothorax (fig. 2, *P*), metathorax (*M*) and abdominal tergites 1-8 (*A*). Here are placed the characteristic ridges, typical for all species of the genus, and on the top of them are slits for the emission of fluid (coelomopores, Blutungsspalten). These ridges on the pronotum are in its hind part, usually four in number, an inner pair of larger and longer ridges, and an outer pair of shorter ones. On the top of each ridge there is a very fine slit, usually firmly closed, but opening when the pronotum is pressed from the sides; this blood-exuding pore (coelomopore) begins somewhat behind the anterior margin of the ridge and ends on the hind margin of the pronotum. The number of the pronotal ridges in *B. multituberculatus* can vary; sometimes there is only one ridge (fig. 3, 1, a deformity), but there can be also as many as 5-6 ridges, because of the appearance of the supplementary ones (4, 6, 7 and 8 of fig. 3). The number of the pores may not correspond to the number of ridges, since they may be simply on the margins of the pronotum (3, 4, 8) and their number can reach seven (8), where there are 5 ridges, while sometimes there may be only one pore (1, 2). On the metanotum and on the abdominal tergites 1-9, there are on the median line peculiar T-shaped elevations; on each side of the elevation, are placed obliquely (seldom straight) large oval convexities, which are largest on the 1-6 segments; on the surface of the convexities (on the metanotum

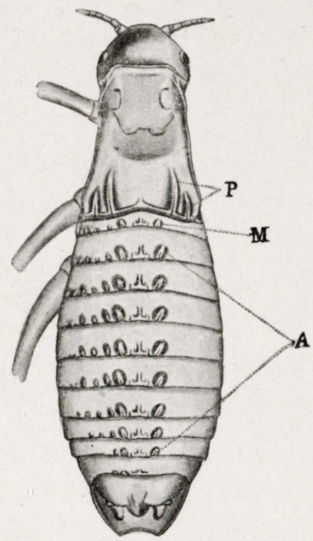

Fig. 2.— Distribution of coelomopores: *P*, coelomopores of the pronotum; *M*, of metanotum; *A*, of abdomen.

and 1-9 abdominal tergites) are also visible the narrow slits-coelomopores; the pores begin somewhat behind the anterior margin of each convexity and reach the hind margin of the corresponding tergite. On the hind margin of each tergite there are, further, some smaller

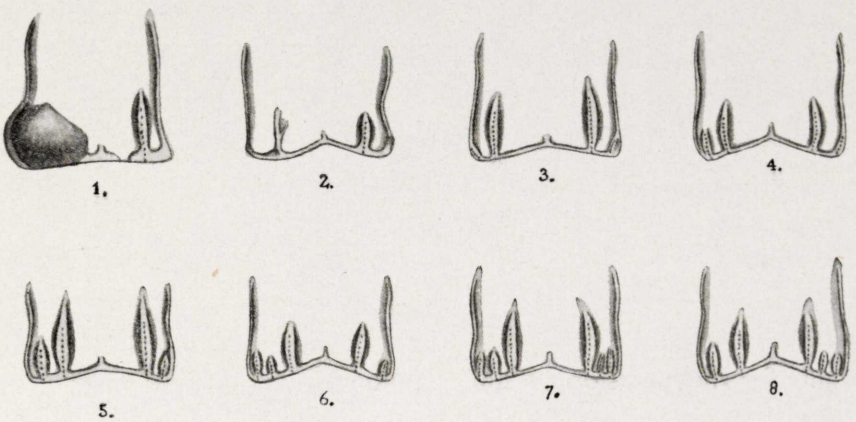

Fig. 3.—Variations in ridges on the pronotum.

rounde tubercles placed in a definite order, but these tubercles bear no slits for the ejection of blood.

Observations on the ejection of blood (Blutaustritt, defensive Blutergus of Vosseler, l. c.) were made by me both on the insects in captivity, and during captures in the field, with the following results.

The fluid ejected by *Bradyporus* in all essential characters, as well as in the structure of its elements does not differ from the blood (haemolymph) taken from the body of the insect. I usually obtained blood from cuts on the abdomen, and the quantity of blood was surprisingly large. Under the influence of air the pale-yellow, transparent blood soon (after 1-1,5 minutes) becomes muddy, and 1-2 minutes later some fibrine-like, slimy-flaked substance appears at the bottom of the glass. The blood has the taste of the white of an egg, with a slight astringent flavour.

The blood exuded from the coelomopores has exactly the same characteristics, and an examination under microscope reveals the same elements (haemocytes) as in the blood from cuts. When coming out from the pores, the fluid is clear, or slightly muddy (because of the large quantity of haemocytes), but already after 0,5-1 minute it becomes quite muddy and the fibrine-like masses are formed; the fluid leaves

pale-yellowish stains on the skin of one's fingers and on paper (in my note-book the stains are perfectly preserved after ten years), smell slightly of grass, or not at all; the taste as described above for the blood from body. There is no other effects on the skin of hands, apart from the yellowish stains, which are easily washed. The process of coagulation is usually completed already 2-3 minutes after the exudation of blood; the fibrine-like flakes involve also the haemocytes and in a watch-glass the blood is clearly separated into two parts -slightly muddy yellowish fluid and the fibrinoid mass on the bottom.

It was perfectly clearly established by my observations, that the haemorrhage in *Bradyporus* is *neither a voluntary, nor even a reflex action*, but the direct result of a pressure, however slight, on the sides of the insect. The pressure causes the coelomopores to open and through them either jets of blood, or drops of it, are ejected. Strong and repeated pressure results in the repetition of the process. When the pressure ceases, the pores close and are sealed by the coagulating blood.

Perhaps, some part in the act of haemorrhage is taken by the contraction of abdominal segments, which gives an additional pressure, but this could not bet noticed. In any case, the extreme abundance of blood in the body of *Bradyporus* ensures a full possibility to eject it with a considerable force through the coelomopores under the influence of external pressure. In the captive individuals the quantity of blood exuded was much less, than in nature, and this can be, perhaps, explained by the unsuitable food, which caused a reduction of haemolymph. While in nature all individuals, even obviously old ones, exuded large quantities of blood when captured, the individuals kept in captivity often lost the ability altogether; thus from 12 males after two-three days in captivity only four were capable of haemorrhage.

Numerous observations on *Bradyporus* in the field convinced me, that it is quite impossible for the insect to eject the blood voluntarily, as I have already said. A frightened *Bradyporus* either remained where it was, or moved clumsily from one branch to another towards the ground, trying to avoid the approaching hand, not to frighten it off by ejecting blood or otherwise. Neither was the haemorrhage provoked by slightly touching the insect at different parts of the body; I succeded even in taking it in hand. As soon as, however, a *Bradypo-*

rus is taken by the sides, particularly by the sides of thorax, and a slight pressure exercised, immediatly the haemorrhage begins.

In the case of strong and well fed insects, the jet of blood can be 3-4, 8-10 and even 13-14 cm. long. At the first moment a slight crackling noise is heard from the opening pores on the large pronotal ridges and the jet of blood can be felt striking the hand for 1-2 seconds. The blood flows on the sides of the body and sometimes foam is formed by the air escaping from the first thoracic spiracle. The fluid in the sun and wind quickly coagulates and forms on the body yellowish smears. Sometimes, ther is no jet and only large drops of blood are exuded.

The haemorrhage is observed in both sexes. I had no opportunity of observing larvae, but on the collection specimens of larvae (30 mm. long) I have found typical coelomopores in the usual places. In the larvae of the first stage I have also found some traces of fine slits on the hind margins of feebly developed pronotal ridges and on the convexities of metanotum and abdomen; whether the pores can function in this stage, I do not know, because the only larva of this stage was taken by me out of an egg and soon died; in any case, the quantity of blood in the body of the larva was considerable.

In the adults the blood is exuded more plentifully on the pronotum, and more often on its larger ridges. Sometimes it is exuded only on one side of the body, while there is no blood, or very little of it, on the other; on one side it may appear as a jet, while on the other only drops are exuded. Less abundant, but still considerable, haemorrhage occurs from the coelomopores on the 1-6 tergites (sometimes 1-7); convexities on the 8th tergite function only seldom, while an exudation of a drop of blood from the 9th tergite was observed by me only once and that on a freshly killed specimen, by strong pressure on the abdomen. The coelomopores of the metanotum exude less blood, than the middle segments of the abdomen.

Repeated pressure on the sides of pronotum resulted in repetition of haemorrhage, but it was less abundant every time. If first time the pronotum was pressed, the next pressure on the abdomen produced less blood, than usual; when, however, only the abdomen was pressed first, this did not affect the quantity of blood exuded from the pronotum at the next pressure on it. This shows, that the greatest quantity of haemolymph in the body is concentrated in the thorax.

Blood from the metanotum is exuded usually only after special pressure on this portion of the body.

The act of haemorrhage does not seem to depress the activities of the insect after it and does not make it more feeble; one old male, after it was taken in hand exuded large quantity of blood, was placed again on the shrub and started singing again after ten minutes; five days later I have found this male (which I have marked) on the same spot.

What can be the meaning of this abundant haemorrhage resulting from pressure ? Can it be regarded as an act of self-defense ? There are no experimental data bearing on the problem in literature, and I was also unable to make exact observations, owing to the absence of suitable insectivorous animals for the experiments. In the circumstances we can only try to find a reasonable theoretical explanation of the phenomenon.

Bradyporus is a heawy, slowly mowing creature, of a coloration which does not conceal it on the background of the steppe vegetation (an exception is offered only by the larvae of the first stage, which are of a greyish coloration homochromous with the ground). This large and fat insect should be a very tempting and easy prey for various insectivores, but we know, that even old, almost invalidated individuals live until their natural death. This tends to indicate, that the haemorrhage must be of value as a defensive act.

Bradyporus, as we know, is unable to eject blood at the approaching enemy, and, besides, the blood is quite harmless. What happens, therefore, must be this. Ejection of strong jet of fluid happens when the insect is caught across its body in the mouth of a bird, or other animal; hard and sufficiently strong chitinous cover prevents an injury to the insect at the first moment, while the jet of blood strikes with some force into the mouth of the animal, streaming into its throat, perhaps also into eyes, nose etc. This happening unexpectedly, the animal drops the insect, and in this way a negative attitude towards *Bradyporus* develops in the individuals of the insectivores, which once tried to catch it; thus the striking coloration of the insect becomes a warning one.

All these suggestions, of course, must be checked in future by direct experiments.

Finally, there are some very unexpected facts, which enable us to regard the haemorrhage in *Bradyporus*, at least partly, as means of the mutual attraction of sexes, but it would be better to describe these facts when discussing the mating habits (see chapter 6).

After an examination of collection specimens of other species of *Bradyporus* (*B. montandoni* Burr, *B. pancici* Br.-W., *B. oniscus* Charp., *B. dasypus* Ill., *B. dilatatus* St., *B.* sp., from Syria) I arrived to the conclusion that the arrangement of coelomopores, as described for our species, is typical for the genus, while there may be slight specific (and strong individual) variations in their number.

It is very interesting, that there is a great analogy in the haemorrhage of *Bradyporus* and of *Pycnogaster bolivari*, in which the blood exudes under the influence of presure in drops from two longitudinal slits on the sides of pronotum (Ebner, 1925).

VI. **Courting and copulation.**

When studying copulation in various Tettigoniidae, I always noticed, that females were more eager to copulate during the first weeks of the adult stage; maturation of ovaria and beginning of oviposition, while not excluding the possibility of further copulations, made them less often, and the females responded to the courting of males less eagerly.

Females of *B. multituberculatus* in August were ovipositing; their ovaria were filled with mature eggs, and spermatheca-with the sperm. They were very unwilling to copulate, in spite of energetic courting and singing by the males; still the copulation was possible, as will be seen later. I was unable to observe the whole process of courting and copulation on one pair and I could form an opinion on the process from several distinct observations.

I have already said above (chapter IV), that females may be found near the bushes on which a male is singing, or coming towards them. Twice I have heard also short, not very loud shrieks emitted by females in response to the call of males. There is no doubt, therefore, that the shrill afternoon songs of males are intended to attract females, which at that time come out of their hiding places and crawl about.

This accounts also for the position of stridulating males on the top of bushes, from where their songs carry farther.

Details of courting I observed only in captivity. Once (at 7 p. m., 31st July) I observed in my insectary-room a female, just completing her meal, to go towards a bush of *Rhamnus pallasii*, where a male was singing; after climbing the plant, the female sat near the male, then crawled close to him, climbed on his back and pressed her mouth-parts to his hind tergites; this posture was interrupted through the female falling down. When a female approaches a singing male, the latter backs and tries to push his abdomen underneath that of the female; the end of his abdomen is then somewhat curved upwards, and he tries to grasp by his cerci (fig. 4), which are sticking sideways, the subgenital plate of the female (fig. 5), by placing the tips of the cerci into small pits at the base of the plate. If he succeeds in that, the female, which stands above the male with the head directed as his is, must lower somewhat her ovipositor. While trying to grasp the female by the cerci, the male opens its genital valves and begins to put forth his genital parts. These acts often ended at that and the pair separated, apparently because the female was not suficiently eager to copulate.

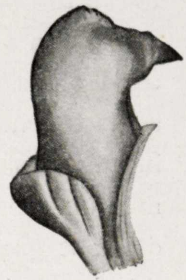

Fig. 4.—Male cercus.

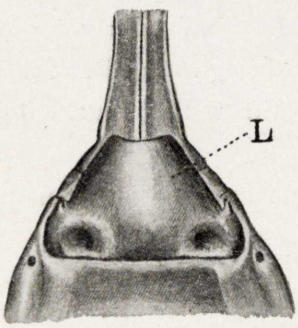

Fig. 5.—End of the female abdomen from below. *L*, subgenital plate.

The sluggishness and indifference to danger, peculiar to *Bradyporus*, enabled me to make some attempts to provoke copulation artificially, by putting a female on a male, and in many cases the males responded, as described, while the females attempted to rub by their mandibles tergites of the male. This latter habit is very interesting, as it offers a supplementary explanation of the phenomenon of haemorrhage. I will now describe exactly my observations on this point.

At six o'clock in the evening of August 13th, as I approached a bush of *Rhamnus*, on which a male *Bradyporus* was singing, I heard some short shrieks coming from the base ot the same bush; this pro-

ved to be a female crawling on the ground. She whas immediatly placed into a small wire cage with three males and, still during the excursion, I saw the following interesting spectacle: the female climbed one of the males from behind and opening broadly her enormous jaws, began to touch with them the tergites of the male, beginning from the middle ones and gradually moving forward; when pronotum was reached, she started irritating the right ridges of the latter; under pressure, the haemorrhage began and the female immediattly started to bite furiously the pronotum, has bitten off a small portion of the hind margin; the blood started running freely and the female began to drink it greedily. When placed afterwards in the insectary room, this female kept all day long amongst grass and bushes, coming out only in the evenings; once I heard it shrieking in response to a call from a male, but there was no copulation.

On the 19th of August this female was placed on to a male, in which I produced haemorrhage by pressure on the sides of the thorax. The female very readily drunk the drops of blood, and begun to touch by her opened jaws the ridges, then she has bitten off a fairly large piece from the hind margin of the pronotum and begun to drink the flowing blood; the male, however managed to throw the female off and to run away.

Only two day later I managed to induce this female to copulate (see below), after she has laid two portions of eggs.

What is the meaning of these facts ? The ability to exude haemolymph exist in both sexes, and the primary meaning of the process is defensive. At the same time, however, the autohaemorrhage is not without an importance in the mating processes. It is known for a number of *Tettigoniidae* and *Gryllidae*, that copulation is often preceeded by the female irritating the tergites of the male, where sometimes even special glands are present, secretion from which serves for alluring the male (alluring gland of *Isophya acuminata* Br. W. and *Oecanthus pellucens* Scop.; Duftorgane of *Troglophilus;* see Engelhardt, 1914, 1915; Seliskar, 1923; Gerhardt, 1913, 1921; Boldyrev, 1915). Haemolymph of *Bradyporus* can also have similar alluring function, apart from the defensive one. The great quantity of blood in the body of *Bradyporus* makes it possible to obtain a good flow of the liquid by even a slight pressure, and it seems that females in na-

ture only seldom resort to biting the male pronotum; at least, I never found males in the field with wounds of this kind, but this must occur occasionally judging by the observations described above.

It is interesting, in connection with the above, to point out, that I observed in *Bradyporus* not uncommonly the cases of *copula inter mares* (which is often observed in other *Tettigoniidae*, as well); one of the males in this case assumes the role of a female copying her behaviour. When as many as 15-20 males were kept in the insectary with 1-2 females, it often happened that a male climbed the back of another one and, broadly opening his jaws, irritated with them the tergites and the pronotum; sometimes an exudation of blood was observed. The behaviour of the male which was underneath, was different: either he behaved as during a normal copulation, protruding his genital parts, or else he went away and the upper male fell, or remained behind. This courting between males is sometimes going on very persistently, the males running after each other, but I never observed the emission of a spermatophore. Once I saw a male irritating by is jaws the tergites of a female, which was occupied by laying her eggs (this may be regarded as *copulatio inversa*), but he soon left her and went away. In all this cases the behaviour of the male playing the female part is very puzzling.

Before describing the copulation itself and the formation of spermatophor, I will give a description of the genital appendages of the male, which were only briefly described for another species (*B. dasypus* Ill.) by Chopard (1920, pp. 138-139, figs. 167, 168).

The perianal region of *B. multituberculatus* (fig. 6) is limited from above by the 10th tergite; in the middle of the latter there is a soft rugulose space and to this space adjoins the supraanal plate; sideways from the latter are placed the cerci, provided with a strong tooth directed somewhat obliquely inwards, towards the two subanal plates, which are at the sides of the anus. All genital parts are normally drawn in into the deep genital fold, which is covered from above by the large subgenital plate. When protruding (during the copulation), these genital parts look like swollen, dirty-yellowish, partly slightly transparent organs, which were called by Chopard (l. c.) genital valves; above them is placed the forked, blackish-brown titillator (epiphallus), which is separated from the perianal region by a thick fold. The ge-

nital valves («penis», as they were called by Brunner, 1876, pp. 8-9; see also Boldyrev, 1915, p. 10) are fairly sharply divided into two parts; the upper genital valves (fig. 6, *s*), which consist of two elongate mammiform bodies directed sideways, and the lower valve (fig. 6, *in*), which is like a broad funnel with the genital opening at its bottom. The funnel is separated from the upper valves by a high ridge, along the median line of which, on the inside, run two folds; side walls of the funnel in the middle of their margins bear small tongue-shaped projections; hind wall of the funnel is elongated also into a tongue shaped, fairly thick appendage, provided with a furrow along its inner side.

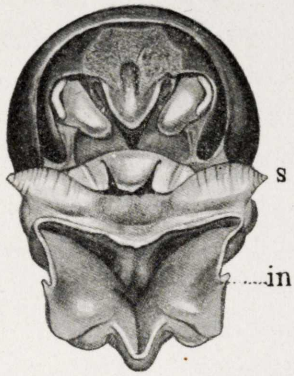

Fig. 6.—End of the male abdomen from behind, with the genital parts protruding. *S*, upper genital valves: *in*, lower genital valves.

Genital valves, especially the lower ones, serve to support the bulky spermatophor, when it comes out of the genital opening of the male and is introduced into the genital cavity of the female (*chambre perivulvaire*, Cappe de Ballion, 1919, p. 18; *receptaculum spermatophorae*, Boldyrev, 1915, p. 10). At the beginning of the copulation the valves (together with the titillator) prepare the now open genital cavity of the female for the reception of the spermatophor; the main part in this belongs, however to the titillator (fig. 7), which is a very strong organ, composed of a transverse plate and a pair of horns, divergent sideways and gradually narrowed to their ends, pointed and somewhat curved backwards and downwards. The titillator serves to irritate by scratching the walls of the *chambre perivulvaire* and, perhaps to enlarge that chamber before the spermatophor (fig. 9, 1, *F)* is introduced into it.

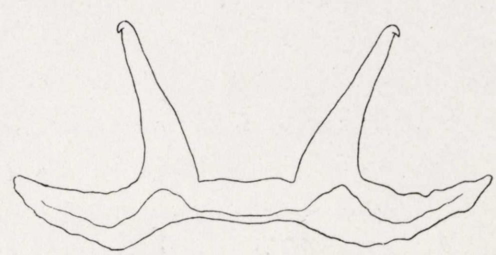

Fig. 7.—Titillator of the male.

My attempts to induce *Bradyporus* to copulate were for a long time unsuccessful. I kept both sexes in my insectary-room, placed

pairs into small cages, tried to place a female on the back of a male, but obtained only the initial stages, without a complete copulation of the sexes and formation of the spermatophor. At last, I saw the complete process of copulation between a male, though old, but still very active, and a female, which I mentioned above and which has already laid 31 eggs; in her ovaria remained still 11 mature and 16 nearly mature eggs. During the day (21 August) the pair was in a cage, the male singing, and the female either sitting quietly, or crawling about and feeding. About 10 p. m. at the temperature 25°C. and by the light of a lamp, I took the pair out of the cage and placed them on my table. Then I placed the female gently on the back of the male. At first both were indifferent, but finally the male started extruding his genital parts (genital valves and titillator), curved the end of the abdomen upwards and introduced the teeth of the cerci into the pits (fig. 5) of the subgenital plate of the female. This took 15-20 minutes.

When the pair joined firmly, their posture was, as follows (fig. 2, Plate I). The male was under the female, with his legs somewhat spread out and with the abdomen pressed to the surface of the table. The female was on the top of the male, with her legs of the first pair resting on the sides of his prothorax; middle legs rested on his mesothorax, or sometimes, on the abdomen; hind legs were somewhat spread out and resting on the table; her mouth was above the hind margin of the pronotum of the male, but she made no movements with them to irritate the ridges on it. The sternum and the abdomen of the female were resting heavily on the abdomen of the male; her abdomen was slightly hanging and curved downwards, so that the intersegmental membranes above became visible; the ovipositor was directed downwards, touching the hind margin of the male subgenital plate and practically resting on the table. The cerci of the male were fixed firmly at the base of the protruded subgenital plate of the female; his genital cavity was broadly opened and all genital valves strongly protruded and touched the lower surface of the ovipositor.

During the copulation I had to support the pair by my hand, since the insects were losing their balance on the smooth surface of the table; this must not happen in nature, where they can clutch at the branches.

The whole process of copulation occupied I hour and 37 minutes;

out of this time an hour and a half were spent on the preparatory acts (rubbing of the genital parts of the male against those of the female) and only 5-6 minutes were taken by the emission of the spermatophor and its introduction into the genital cavity of the female. During the preparatory acts the male genital valves now were somewhat removed from the ovipositor, revealing the blackish titillator, then again they became swollen and pressed tightly to the base of the ovipositor, rubbing against it with a distinct scratching sound, produced by the pointed ends of titillator rubbing the inner surface of the genital cavity of the female. The abdomen of the female, during the rubbing also made some synchronous notions, the end of the ovipositor sometimes almost touching the table. Half an hour after the beginning of copulation the rubbing movements began to be more energetic at times, and the male backed under the female, still more strongly protruding his genital parts. At last, his genital parts were protruded extremely strongly and firmly grasped the base of the ovipositor; this was repeated 15 minutes later and after that his genital valves did not separate from the ovipositor; they slightly moved, swelled, and finally from underneath them a large drop of clear yellowish liquid appeared and spread over the base of the ovipositor. This took about a minute, and during the next minute from beneath the male valves appeared a pair of large, oval, cream-coloured structures—so called *supplementary reservoirs* (fig. 8, *R*), which occupied places on the two sides of the ovipositor. A minute later the female rose somewhat on her legs and from the still moving (though less energetically) valves of the male appeared in 2-3 minutes an enormous rounded, dirty-yellowish-white structure (fig. 8, *Sp*)—the *spermatophylax*, which took the place below and in front of the supplementary reservoirs. At the base of the ovipositor, above the supplementary reservoirs were visible muddy-white lobes (fig. 8, *n*) which served to fix the spermatophor. Since during the fixing of the spermatophor in the genital cavity of the fe-

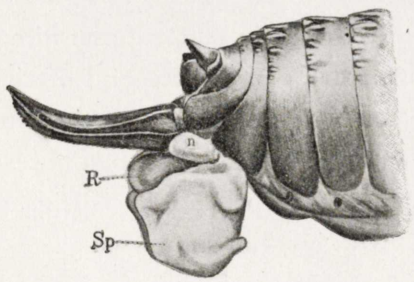

Fig. 8.—End of abdomen of the female with the spermatophor *in situ*. *n*, lobes; *R*, supplementary reservoirs; *Sp*, spermatophylax.

male the so called flask with sperm is introduced, this process not being visible to the observer, we must conclude that the whole process of emission and fixing the spermatophor occupies not less than 5-6 minutes.

During the emission of the spermatophylax the male moved slightly forward, and after the spermatophor was emitted, he separated from the female, crawled a short distance and produced a short trill, repeating it after some two minutes. The genital parts of the male were still protruding and resumed their normal appearance only after some nine minutes. Placed into a cage, the male started singing with interruptions.

The behaviour of the female after copulation I was unable to observe because I wanted to preserve the spermatophor for its study *in situ*, an the female was prevented from touching the latter for an hour, then dropped into alcohol. By the analogy with other *Tettigoniidae* we can assume that the female, after separating, must start devouring the spermatophylax, which plays the part of a barrier, preventing the female from destroying the flask with sperm before the latter has flown into the receptaculum seminis.

VII. **Spermatophor and sperm.**

I have already published some preliminary observations on the structure of spermatophors of *Bradyporus* (Boldyrev, 1915, pp. 107-108).

In *Bradyporus*, and in the *Tettigoniidae* generally, the spermatophor before the beginning of the copulation lies in the genital organs of the male in half-formed condition, and assumes its final shape only during the first (preliminary) period of copulation; in this respect *Tettigoniidae* differ from *Gryllidae*, in which the spermatophor lies perfectly formed in the so called «spermatophor pouch» of the male (Cholodkovsky, 1910, p. 76) long before the copulation. Half-formed spermatophors of *Bradyporus* I used to obtain by chlorophorming the males slowly, when they emitted at the moment of their death these spermatophors; it was also possible to obtain such spermatophors by

dissecting the males, or by gently pressing the abdomen of a freshly killed male.

The terminology of the parts of *Tettigoniidae*-spermatophors has been established by me in a definite form in another paper (1915, pp. 8-10) and I am using it here without any alterations.

The spermatophor of *B. multituberculatus* taken from a fertilised female has the following parts (fig. 9): basal portions, consisting of a

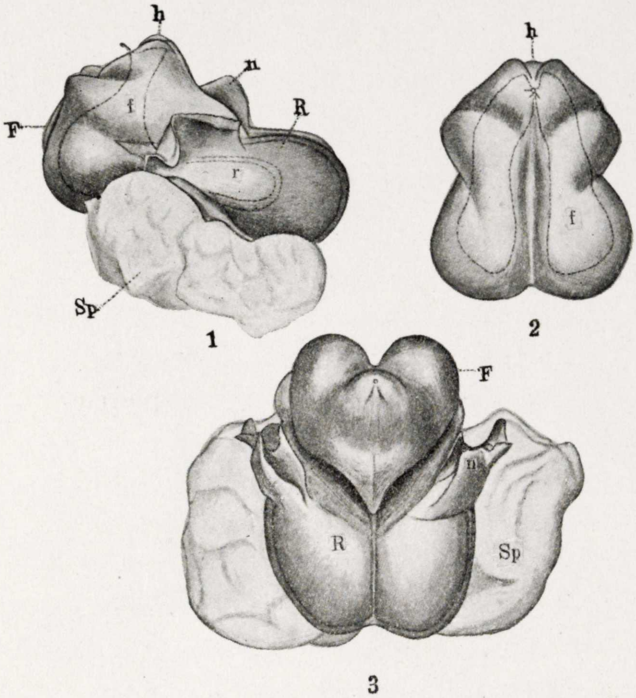

Fig. 9.—Spermatophor: 1, side view; 2, flask, front view; 3, from above; *h*, neck of the flask; *F*, flask; *f*, cavity with sperm; *n*, lobe; *R*, supplementary reservoirs; *Sp*, spermatophylax.

«flask» (*F*) and supplementary reservoir (*R*), and the protective apparatus, or spermatophylax (*Sp*). Thus, the spermatophor of *Bradyporus* belongs to the category of, so called, compound spermatophors, which are peculiar to most of the *Tettigoniidae*. When the spermatophor is in its place on the abdomen of the female, only the spermatophylax with the supplementary reservoirs and the lobes (*n*), which fix the spermatophor to te base of ovipositor, are visible, while the flask is entirely concealed in the genital cavity of the male.

The flask (*F*) is very massive, with the walls thick, solid, muddy-

yellowish, slightly transparent; its top portion, the neck (*h*) is feebly developed and bears two lateral tubercles; on the front side of the flask there are two large rounded antero-lateral convexities; along the middle runs a deep furrow which passes also on to the lower side of the flask and divides it into the right and left halves; the flask is broader in its lower portion. Inside the flask are dimly visible the outlines of two elongate-pyriform cavities, filled with whitish sperm (*f*); from each cavity a little below its upper margin begin two ducts, which then unite and open in front of the apical part of the neck (fig. 9, 1, an arrow shows where the sperm comes out). When the flask rests in the perivulvary chamber of the female, the opening of the flask exactly adjoins the opening of the channel leading into the cavity of the spermatheca.

The paired supplementary reservoirs (*R*) are very firmly joined to the hind wall of the flask; they are oval in shape and bear on their upper and hind surface a median furrow; their walls are fairly thick and hyaline; the reservoirs are separated from each other by a median septum. At the moment of fixation of the spermatophor on the female, the cavities of reservoirs are creamy-white in colour, but after a few minutes the cavities become clearer (the clearing beginning from their periphery) and after an hour they become opaque-hyaline, the white tint remaining only in the deepest parts of the reservoirs, near the septum (*r*). What is the function of the supplementary reservoirs in the *Tettigoniidae* generally and what is their relation to the sperm cavities of the flask-this question still remains unknown (discussion of the problem see in my paper, 1915, pp. 187-188). It was still more difficult to form am opinion on the function of the reservoirs in *Bradyporus*, since the only spermatophor in my posession was examined *in toto* (cleared in clove oil), and it was impossible to make sections as it was too much hardened by alcohol.

The lobes, which serve to fix the spermatophor on the base of the ovipositor of the female (figs. 8, 9, *n*), are, when the spermatophor is freshly fixed, fairly viscid, milky-white and their surface copiously moistened with muddy-hyaline fluid.

The spermatophylax (figs. 8, 9, 10, *Sp*) is the most massive part of the spermatophor; it is firmly connected with the basal portion where the supplementary reservoirs join the lower part of the flask.

The spermatophylax covers the supplementary reservoirs from below; in front it come into close contact with the subgenital plate, which stands vertically and is even somewhat pressed into the substance of the spermatophylax. In its shape the spermatophylax is irregularly round, with a furrow along the median line behind and below; below and in front it has short appendages; the surface of the spermatophylax is covered by rather symetrically distributed pits and convexities. Spermatophylax is fairly firm, elastic, sticky and moist to the touch; in colour it is shining, milky-white, slightly opaque; the shine, moisture and stickiness are specially noticeable in its anterior portion; where the subgenital plate is impressed into it, the substance of the spermatophylax projects like hyaline sharp ridges. The surface of the subgenital plate is covered by some special liquid. When a spermatophor is taken away, it becomes visible that the subgenital plate was firmly embedded into the substance of the spermatophylax, which is very important for the fixation of the spermatophor in its place.

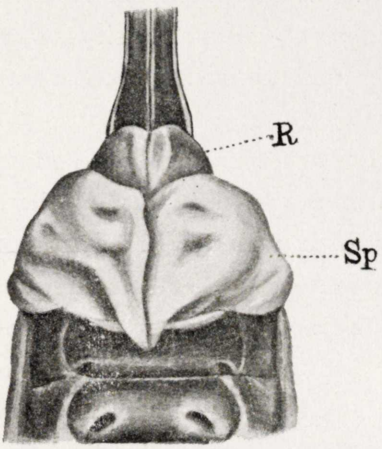

Fig. 10.—End of the abdomen of female with a spermatophor *in situ*. *R*, supplementary reservoirs; *Sp*, spermatophylax.

The function of the spermatophylax is to prevent the female from devouring the basal portion of the spermatophor until the sperm from the latter is transferred into the receptaculum seminis; the sticky and viscous substance of the spermatophylax keeps the mandibles of the female busy for a long time, and the first parts of it, which come into contact with the mandibles are exactly the most viscous and sticky ones.

The spermatophor of *Bradyporus* is extremely massive and exceeds in size those of other *Tettigoniidae*, so far described. Its measurements are as follows. The height of the flask 8 mm.; its maximum width (at base) 7 mm.; width in the upper part 6,5 mm.; maximum length 8 mm. The maximum length of the supplementary reservoirs (along the sides) 8 mm.; their minimum length (along the median line) 4 mm.; width of the two reservoirs at the base 9 mm.; length of the

lobes 6 mm.; height 3 mm. Maximum diameter of the spermatophylax 16,5 mm.; its height 10 mm.; length 9 mm.

When examining the large rounded receptaculi seminis of all the females captured by me, I always found in them some thick, muddy-white sperm, which consisted from a mass of spermia and a great quantity of granular intervening substance. The spermia are usually in feather-like groups (spermatodesms) with a central axis, but I have never observed the spermatodoses, i. e., round ampullae with an elongated neck, formed in the receptaculum seminis and separating the sperm into portions (doses). The spermatodoses are known for a number of other *Tettigoniidae (Decticinae*, *Tettigoniinae*, *Saginae*), and it is possible that an examination of larger material from earlier copulations would result in their discovery in *Bradyporus*, as well.

When live sperm is examined under microscope, one can see the energetically moving spermatodesms, which swim about in the serose fluid of the receptaculum by means of incessant synchronous movements of the tails of spermia. The spermia are attached symetrically to the central axis of the spermatodesm, forming with it an angle; the axis is long, straight (seldom a litle bent). Some of spermatodesms consist of not more than ten spermia, but others contain scores of them, and perhaps even more than a hundred; there are also some solitary spermia, or forming pairs, and in these one can see a special short appendix at the end of the head—a hook, which apparently is used when a spermatodesm is formed. The spermatodesms are rather durable; they remained whole when put into water for 2,5 hours and could be preserved well in the 90 per cent alcohol. The intervening substance consists of a mass of rounded bodies, mixed with spermia, but in some cases larger groups of the same round bodies can be also seen.

Summarizing all what has been said above about the copulation processes in *Bradyporus*, we can give the following diagnosis, which would fit into the scheme given by me on another occasion for several subfamilies of *Tettigoniinae* (Boldyrev, 1915, p. 225):

Subfam. *Bradyporinae* (genus *Bradyporus*).

The copulation posture: the female on the top of the male, both with the heads looking in the same direction.

Spermatophor compound, with a fully developed spermatophylax;

flask with two cavities, with the neck feebly developed, and with supplementary reservoirs.

Spermia in feather-like spermatodesms (when in the receptaculum of the female).

In these characters *Bradyporinae* may be placed near *Decticinae*, *Tettigoniinae* and, partly, *Saginae;* the copulation posture resembles that in *Onconotus* (*Tettigoniinae*).

VIII. **The egg and oviposition.**

The ovipositor of the female *Bradyporus* (fig. 8) is moderately long (14-16,5 mm. along the straight line from the tip to the base), slightly curved and narrowed towards the pointed apex, the lower margin in the apical fourth being coarsely serrate; in the living females (and in most of the collection specimens) the valves of the ovipositor are never open, as it was described by Brunner in the generic diagnosis of *Callimenus-Bradyporus* («valvulis apice hiantibus»; Brunner v. Wattenwyl, 1882, p. 251). During the oviposition the ovipositor may form nearly a right angle with the axis of the body.

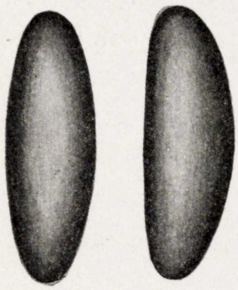

Fig. 11.—Egg in two positions (*A* and *B*).

A mature egg (fig. 11), freshly laid, or taken out of a female, is elongate-oval, equally rounded at both ends. When regarded in one position, both sides seem to be equally convex (*A*), but turning the egg round its long axis, one side appears to be more convex, than the other (*B*). Length ot the eggs 8-8,5 mm., diameter 2,6 (smaller diameter) to 2,8 (larger diameter). Once I have found, on dissecting a female, side by side with the ordinary eggs one gigantic egg—10 mm. long and 3,5 and 3,6 in the two diameters.

The chorion of the egg is unusually thick (not less than 0,2 mm.) and strong, and covered with a peculiar honey-combed sculpture (fig. 12); the cells of the sculpture are fairly uniform on the sides of the egg, but nearer to one end they become larger, while at the other end they are irregular, smaller and seem to form a group round a cen-

tre. This sculpture of eggs was recently described and figured for *Bradyporus pancici* by Cappe de Baillon (1919, p. 113, pl. VIII, fig. 92).

The colour of the egg is dull greyish-brown, but a strongly moistened egg becomes dark-brown; the inner surface of the chorion is shining brownish-ochraceous; under the chorion lies thin, hyaline, or slightly opaque, membrane (Dotterhaut). The contents of the egg is yellowish, semi-hyaline, viscous and sticky, with numerous inclusions (drops, small balls) of nutritive materials. In the developing eggs the whitish embryon is well visible on the hyaline yellowish background of the yolk. In the eggs which die during the development, the contents becomes dense, like curdled milk, sometimes yellow, or musty and the chorion often cracks.

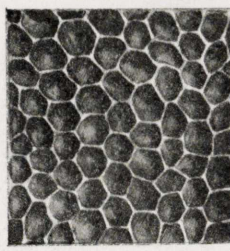

Fig. 12. — Structure of the chorion of the egg.

The eggs of *Bradyporus* in the nature undoubtedly have to suffer sharp fluctuations of meteorological conditions, since they cannot be laid very deeply into the soil, the ovipositor being only 17 mm. long. It is not impossible, that the deep honey-combed sculpture of the chorion has a protective function, the air accumulating in its cells acting as a protective layer against fluctuations of temperature and moisture.

The oviposition I observed only in the cages. I have no data which would enable me to form an opinion on the total productions of ovaria, since I began my observations when the females captured in the field may have already laid part of the eggs. Still, I find it useful to give some figures, observed on the females captured during the period from July 29th to August 13th.

Female taken 29.VII; dissected 7.VIII; in her ovaria were 31 fully mature (brown) and 20 nearly mature (pale) eggs, i. e., altogether 51 eggs, which might be laid in the same season.

Female taken 1.VIII; laid on 5.VIII 16 eggs; disected 9.VIII and 24 mature and 28 nearly mature eggs found; full production during August may be stated as 68 eggs.

Female taken 3.VIII; dissected 13.VIII; 64 eggs found, 47 of them mature and 17 nearly so.

Female taken 13.VIII; laid in captivity on 19 and 20.VIII 31 eggs;

on dissection 11 mature and 16 nearly mature eggs were found, i. e., altogether there were 58 eggs.

Thus, the total number of eggs, which may be possibly laid during August by one female is at least 51-68. The maximum amount of eggs in the ovaria found by me was 57; that was in a female, which lived in the laboratory of the Essentuki Plant Protection Station since 8.VI.1924 and was disected by me on 12.VIII of the same year with the above result.

Oviposition in captivity I observed on three different occasions: 5.VIII, between 12.15 a. m. and 2 p. m.; on 19.VIII, between 6.30 and 7.45 p. m. and on 20.VIII, between 8.30 and 10.30 p. m., always in small cages, where sods of steppe soil with plants of *Stipa capillata* were placed. Nearly in all cases the females prefered for oviposition not the horizontal surface of the sods covered with grass, but the vertical surface of bare earth. Catching with her two first pairs of legs at the upper margin of the side of a sod, and resting with her hind legs on the floor of the cage, the female sat in a vertical position, head upwards; bending then her ovipositor under the right angle to the body, she inserted in into the sod near to the floor of the cage. I have not noticed the beginning of oviposition and was unable to estimate the time taken by the whole process, but the part I saw occupied 1,75 to 2 hours. At first the female sits motionless, with the ovipositor inserted into soil right to its base; segments of the abdomen now inflate, now contract, which corresponds probably to passing of eggs from genital ducts into the ovipositor; sometimes slight movements of the terminal segments are seen, connected witch the ovipositor itself, and this motionless condition lasts 1 hour 10 min. to 1 hour 30 minutes, the female only from time to time moving a little the ovipositor in its hole, without taking it out. During the last half hour of the oviposition, these movements become more often and more energetic. At last, about five minutes before the end the female takes the ovipositor out and begins to scratch the surface of the soil by it, moving it forward and backward; from time to time she strikes the soil with the ovipositor, perhaps, in order to separate some particles of the soil and to conceal better the traces of oviposition. Finally the female crawls away and it may be seen that the tip of the ovipositor is covered with moistened particles of soil. The fluid is a product of a

special tubular gland, opening at the base of the ovipositor; it is secreted in large quantities during the oviposition, so that the soil around the eggs becomes moistened. The number of eggs in one group (a single observation) is 15-16, and they are firmly connected with each other and with the sorrounding soil by that secretion, so that the whole group forms an irregular ball, sometimes rather firmly glued by one of its sides to the wooden floor of the cage. The position of eggs in the ball is different, but the majority of them are lying close to each other. This group of eggs cannot be regarded, however, as a structure of the same kind, as the egg-pods of *Acrididae*, because on being placed in water the particles of soil separate from the eggs and the group falls to pieces.

IX. **Development of eggs and hatching.**

The eggs laid by my females in the Caucasus in 1917 were taken by me to Moscow, where I hoped to obtain larvae in the spring or early summer of 1918, but quite unexpectedly the eggs proved to be very sensitive to the external conditions, while, on the other hand they exhibited a remarkable ability to be in a diapause (suspended development) for the period extending over several years. This caused my observations not to be completed until April 1923.

External changes in the egg during the embryonal development consist in the gradual increase of the size and changes in the shape. The egg, when freshly laid, is 8-8,5 mm. long and 2,6-2,8 mm. in diameter, while before hatching the figures are 8,8-9 mm. and 3,4-3,6 mm. respectively. The shape alters by one end of the fully mature egg (with the embryon completely developed) becoming more rounded, than the other, and more inflated, sometimes not quite symmetrically.

The eggs were placed into flower-pots at the depth about 17 mm., in sifted soil, which was moistened periodically and kept at different temperatures. A small part of eggs did not develop, while the rest either developed slowly, or rested in a diapause as I was able to see by periodic examinations of eggs.

Although some of the eggs contained fully developed embryons, I was unable to hatch a single larva, though embryons exhibited signs

of life and in one case I even observed the first moult, which occurs immediately on hatching (Embryonalhäutung; La Baume, 1918, p. 168). The extraction of developed embryons was very difficult owing to the strong and thick chorion and I used for it a needle and sharply pointed forceps. Normally the ruture of the chorion must be done by the larva by means of the apparatus, recently described by Cappe de Baillon (1919, pp. 198-203) for a number of *Tettigoniidae* under the name of «lame de rupture». As in other *Tettigoniidae*, «lame de rupture» in *Bradyporus* can be found on the embryonal skin (Embryonalhaut, mistakenly called by many authors amnion), in the middle of the frons, beginning at the level of the upper third of the eyes and reaching the base of the labrum, where a spoon-shaped space is formed and along its middle runs a brown raised ridge, which is the «lame de rupture»; it is 1,4 mm. long and its upper margin is sharp and serrate. During hatching, the contractions of the cervical ampulla set into nodding motion the head of the larva and the «lame de rupture» cuts and saws through the chorion. My larvae were apparently not sufficiently strong (or the temperature was not high enough) to rupture the chorion. The same cause prevented their embryonal moult, though I placed the larvae taken out of eggs into a thermostate at a temperature 25-27° C. and sufficient humidity and partly covered them with soil to give them support. Only in one case a larva managed to throw off its embryonal skin, but not successfully, with a resulting deformity; it lived after that only about three days. This larva of the first stage was coloured above greyish resembling the colour of ground; it was 6,6 mm. long (a full description of the larva will be given by me elsewhere).

When the larva is still in the chorion, the typical pattern is already visible, while the general colour is that of the larva of the first stage so that a larva hatches already coloured, and in the next few hours only the intensity of coloration increases.

The embryonal skin is thick, opaque-hyaline, covered on the surface by numerous minute rugosities, which help during hatching. The rupture of the embryonal skin occurs with the help of the cervical ampulla, as usual in Orthoptera.

During the development in natural conditions, the eggs of *Bradyporus* in the Northern Caucasus, being very near the surface of the

soil, must undergo the influence of long droughts (during the second half of summer and early autumn), soaking rains (late autumn) and prolonged frosts (winter). In my experiments with the eggs I could not, of course, reproduce exactly all these conditions, the more so, that during the period 1917-1923 there was in Moscow a shortage of fuel and interruptions in the supply of gas and electric current, which did not permit me to arrange really exact experiments. Apart from that, diapauses in the development of eggs introduced further unexpected complications into the original scheme of experiments.

The data obtained during the experiments are summarised below, though they permit only few conclusions.

I. One egg (laid August, 1917) kept dry without soil, at the room temperature (15-17° C.) for five months; on one side appeared a deep concavity; on 18.I.1918 the egg placed into moistened soil, and the concavity remained without change, but a dissection (17.IV.1918) showed that the contents of the egg (the plasm and reserve materials) preserved its normal consistency and freshness.

II. 2 eggs (laid on 5.VIII.1917) kept dry without soil at the room temperature for 3,5 months, and on their sides concavities appeared; they were then placed into the soil periodically moistened, at the room temperature (7,5°-16° C. in winter, 20-26° at other seasons). After a month the concavities disappeared and the eggs became normal in shape. Towards the middle of Juli, 1920 the eggs somewhat increased in size (8,6 by 3,2 mm). At the end of August 1920 one egg was dissected and found dead; the contents was mouldy, dark yellow. The second egg dissected on 23.XI.1920.i. e., 3 years and 3,5 months after it was laid; its size was 8,4 by 3,4 and it contained a large quantity of fresh reserve yolk, and an embryon 3 mm. long with the rudiments of extremites.

Conclusions from the experiment I and II:

1) The eggs can stand, without losing their ability to develop, a very long drought. 2) It is not necessary for the development of eggs to subject them first to the influence of temperatures below the freezing point. 3) The development may go very slowly.

III. 28 eggs (laid on 19-20.VIII.1917) kept for 1 month and 10 days at the room temperature (15-17°), without moistening, in the same sod of soil, where placed by female. On 29.IX.1917 they were

laid singly at the depth of two cm. in the moistened soil. Until February 1918 the eggs were kept at the temperature 5-12° C., but were put once for two days into the temperature 0,5° to 2,5°. From February to November 1918 the eggs were kept at 16-18°; then for one month (25.XI to 26.XII.1918) they were placed into a room without heating, where the temperature fluctuated between 9,5° to 6°; during five days of this period the eggs were subjected to light freezing (between—2,5° and 10°); then they were transferred into a temperature 7,5° to 11°, and from the first of January 1919 they remained in the laboratory (between 7,5° and 24°) until May 1920. No larvae hatched from the eggs during all this time. Dissections of eggs for control were made on 10.X.1918, 19.IV, 3.V and 26.X.1919 and in all cases it was observed, that the eggs were fresh and without any sign of developing embryon. Four eggs perished from accidental causes.

Thus, the eggs remained fresh and not developed for 2 years and 8 months, trough they were subjected to slight drying and freezing; percentage of eggs which perished was very small. For further experiments I divided these eggs into three lots, viz. III*a*, III*b* and III*c*, which were subjected to different treatment, as follows.

III*a*. 5 eggs left in the laboratory, in periodically moistened soil, at the temperature 10-26°. Two of the eggs perished, and the remaining three were dissected one after another, with the following results: one egg dissected on 10.XI.1920; contents without changes, no development; second egg dissected on 15.I.1922 and an embryon 3,4 mm. long found in it, while there was still large quantity of yolk; the length of the egg was 8,4 and the diameter 3,4; third egg dissected on 7.IV. 1923 (5 years and 7,5 months after the laying!); its size was 8,2 by 3 mm., shape as in the egg freshly laid; contents fresh, without any trace of embryon.

It is clear from this experimet, that. 1) An egg can rest for, at lest 5 years and 7,5 months without any development of embryo, i. e., in the diapause; 2) eggs stand freezing to 10°, without loosing their ability to develop; 3) eggs laid by the same female at the same time and subjected to the same conditions may develop at different rate; 4) the retarded development of eggs cannot be speeded up by frezing.

III*b*. 7 eggs were kept from 30.IV to 3.IX.1920 in a jar with soil, partly sank in the ground on a very well insolated spot, i. e., they were subjected for four months to the influence of natural conditions, as regards temperatures, insolation, rain, etc.; the summer was dry and hot, but no larvae hatched from the eggs. One of the eggs was dissected on 8.VII.1920 and found to contain a developing embryon 4 mm. long (the egg was 8,4 by 3,4 mm.). Another egg (8 by 2,8 mm.) contained plasm and no trace of embryon. At the same time, there were eggs in the lot as large as 8,8 by 3,6 mm., i. e., of maximum size (not dissected), which shows that the development was going on not at the same rate in the case of individual eggs.

After 31.IX to 17.IV.1920 the eggs were kept in the room temperature (14-18°). One egg dissected on 10.XI.1920 contained a fully formed embryon, which filled all the cavity of the egg, but was still of pale colour with only the eyes sligthly pigmented and with the brown «lame de rupture» standing out sharply against the white frons; this embryon was 3 years and 2,5 months «old», counting from the oviposition.

After the eggs hibernated in the room, the remaining three of them were again (in the spring of 1921) taken outdoors and remained there until 26.VIII. One of them dissected on 10.VI contained an embryon 3,5 mm. long. Two other eggs attained in August the maximum size (8,8 by 3,4 mm.), but no larvae hatched from them. They were dissected by me (after being kept in the room temperature from 26.VIII to 11.XII) and found to contain perfectly developed and fully pigmented larvae included into embryonal skins; when placed in the temperature 27° their abdominal segments were observed to move and the cervical ampulla to inflate. The development of these larvae occupied 4 years and 3,5 months, though it was not impossible that they were lying in the eggs fully developed for 2-3 months and only the insufficiently high temperature of the room prevented their hatching.

What can be deducted from these data?

The development of eggs laid by one female in this case also was very inequal, though they were kept under natural conditions and under strong direct insolation; part of the eggs developed only after two seasons under those conditions; it is possible to ascribe to the influen-

ce of high temperature the acceleration in the development after the first season (see dissection of 10.XI.1920).

III*c*. 5 eggs were kept from 6.IV to 10.VII.1920 in moistened soil on a window looking south, under direct sunlight; from 10.VII to 24.IX they were kept under natural conditions; in IX, after the first frosts taken back to the laboratory. The size of the eggs early in XI was 8-8,4 by 3-3,2 mm., while early in July of the same year they were 8 by 3-3,2 mm. Hibernation (X to IV) occured at a low temperature (from 0,5 to 6°), and eggs dissected on 10.XI.1920 contained a embryon 3,5-4 mm. long. During the spring and the summer of 1921 (from 17.IV to 26.VIII) the eggs were in the open, but after the first frost (1°) they were taken into laboratory. Dissection of all eggs of this batch on 11.XI.1921 showed that two of them were dead and three alive and containing pigmented and ready to emerge larvae. One of the larvae placed in the temperature 25-27° shed its embryonal skin and lived nearly three days more; two others, in spite of all efforts, could not moult. In this case also full development of eggs occupied 4 years and 3,5 months.

IV. 13 eggs, laid on 5.VIII.1917 were kept for two months without moistening in the same sod of turf, where they have been placed by the female; there were no concavities on the surface of the eggs in spite of that. After that, the eggs were kept always in moistened soil, two centimetres under the surface, and during the period from 7.X.1917 to V.1920 they were subjected to the same conditions as the eggs of the lot III (se above), i. e., mostly in the room temperature, but with occasional slight freezing (down to 10°). Two eggs perished; one, dissected on 6.IV.1920 was alive, but not developing. After 13.V.1920 the eggs were divided into two lots, IV*a* and IV*b*.

IV*a*. 4 eggs remained in the laboratory until 20.IV.1921, at the temperatures ranging from 10° to 26°; measurements of the eggs on 8.VII.1920 showed an increase in their size to 8-8,2 by 3,2-3,4 mm.; when one egg was dissected on 10.XI.1920 an embryon 2,6 mm. long was found (i. e., after 3 years and 3 months since the egg was laid). From 20.IV to 26.VIII.1921 the eggs were kept in the open and in August their size was 8,4-8,6 by 3,6 mm. During the winter the eggs were in the laboratory until 25.IV.1922. One egg opened on 15.I.

1922 and a fully developed and pigmented larva was found (after 4 years and 4,5 months since the egg was laid), which looked normal, but showed no movements. The remaining two eggs I subjected during the period 15.I-28.I.1922 to the temperatures 19-21° and up to 44°, trying, without any success, to hatch the larvae. One of these eggs, when dissected on 28.I contained a large embryon which occupied two thirds of the egg, the remaing third containing yolk. The last eggs of this lot, after remaining in the room temperature until 25.V.1922 (when it reached the size 8,6 by 3,4 mm.) was subjected to the natural conditions until 25.VIII; then again taken into laboratory and dissected on 7.IV.1923; it contained a larva ready to hatch, dead but absolutely fresh, i. e. it probably only just died being unable to get out of the egg shell; it was not impossible that it was fully developed already in the autumn, since the egg was on 15.XI.1922 of the maximum size (9 by 3,6 mm.). Still this case is one of a very slow development which took 5 years and 8 months since the eggs was laid, in spite of the high temperature and direct insolation during two seasons.

The rate of development off eggs in this lot was also very unequal.

IV*b*. 6 eggs were from 13.V to 24.IX.1920 kept under natural conditions; after three frosts in September they were taken on 24.IX into the laboratory; their size was at that time 8,2-8,8 by 3-3,6 mm., i. e. their development went unevenly. In the laboratory (room temperature) they remained until 18.IV.1921, when they were examined. Four of them were found of normal shape, but on two others were depressions on the sides (the soil in the jar dried a little during the last weeks); in these two last eggs, with depressions, were found larvae ready to hatch, but dead because of the dryness; apparently they developed already in the autumn, and the whole development in this case took not less than 3,25 years (the eggs were dissected 3 years and 8 months after deposited), which was the shortest period of development obtained in my experiments.

The remaining 4 eggs from 18.IV to 26.VIII.1921 were again kept in the open and reached the size 8,2-8,8 by 3-3,6 mm. The winter they passed in the laboratory; one of them was dissected on 16.I.1922 and a fully developed larva with feeble signs of life found; the development of this larva occupied 4,25 years, since it was, obviously, ready in autumn; one of the eggs was dead.

Two last eggs, after hibernating in the laboratory, were again transferred into the open, where they remained from 25.V to 15.VIII.1922. After another winter in the laboratory, the eggs were dissected on 7.IV.1923; one was dead; another did not change its original shape and size, while its contents was quite fresh and showing no trace of development. This egg remained in a diapause for 5 years and 8 months!

Sumarising all these data, we can state that the shortest period of development in the experiments was 3,25 years, while the development was extended in other cases to 4-4,5 and even over 5 years. An egg can remain fresh and alive, but without any trace of development, in the state of a diapause, for 5 years and 8 months.

What preliminary conclusions can be made from all these data with regard to the development of the eggs of *Bradyporus* under natural conditions in the places of its normal habitations in the Northern Caucasus and South Russia? Is it possible that there also the development retards and the diapauses occur? Can the eggs there complete their development in one season, as it is usual for other *Tettigoniidae*?

The eggs of *Bradyporus* can be laid already in the middle of the summer and these early eggs have before them a long period of hot and dry weather of the second half of summer; the eggs laid later in the summer are in a worse position in this respect. When, after a long period of cooling (late autumn and winter) the rapid southern spring comes, the eggs receive a strong impulse to the further development. All this, taken together, can ensure the development of, at least, the earlier laid eggs during one year. At the same time, there is no reason to think, that the retardation of development (perhaps for two seasons) cannot occur in the eggs laid at the end of the season. Also, a diapause (if not so prolonged, as in the experiments) is not impossible even for a part of the eggs from the same batch, since this phenomenon does not seem to depend much on the external factors.

In any case if all my observations on the development of eggs near Moscow may lead to the conclusion, that the retardation of development and the diapause may be due to abnormal conditions, it is still necessary when studying their development in the normal habitat of

the species, to keep in mind the possibility of similar phenomena, which are of exceptional interest in connection with the study of factors of embryonal development of insects in general.

X. Problem of the extinction of representatives of the genus *Bradyporus* in Russia.

Already Lindeman (1902, p. 206) wrote, that *Bradyporus* in Russia is an insect «apparently dying out». Still more definitely it was put by Uvarov (1915, p. 93) who said: «There is no doubt, that *Callimenus* is on its way to extinction, which is caused mainly by the cultivation of the virgin steppe, without which it, for some reason, cannot live.»

From the literature (Uvarov, 1915, pp. 92-93) and my own observation on *Bradyporus* in the region of its permanent habitation, it may be definitely concluded that this curious insect is ecologically most closely connected with the virgin steppe, where there are groups of small bushes and of tall coarse steppe grasses, which offer *Bradyporus* good shelter from the heat and refuge from its enemies; they also serve for the afternoon songs of the males.

The Balkanian species (*B. dasypus* Ill., *B. pancici* Br. W.) exhibit a great similarity with the Russian species, also living in the groups of shrubs and coarse grasses (*Ilex*, *Sambucus*, *Marrubium*, *Carduus*, *Paliurus*).

When the steppe is cultivated and the shrubs, coarse grasses and weeds cut down, *Bradyporus* loses its places of refuge and is subjected to unfavourable influence of heat, etc. Temporarily they find suitable places on the slopes of ravines, where cultivation is impossible, but even from there they are finally driven out by cattle and by man, who cuts down the last bushes. Sometimes *Bradyporus* can occur also in the cultivated fields, but its occurence there is only temporary, and once the harvest is collected, the insects are exposed to heat and to its enemies, while many of them are killed under wheels of waggons and carried away from the field with the sheafs. Cultivation is also very unfavourable to *Bradyporus* because its eggs are laid not deeply

in the soil and they are either ploughed under too deeply, or exposed on the surface, where they perish from heat, frosts and enemies.

All this makes it easy to understand why *Bradyporus* already disappeared from those districts where the steppe is nearly all cultivated, as is the case in the Ukraine and in some districts of the Northern Caucasus. At present *Bradyporus* still lives and is fairly abundant in some parts of the Don province and in the Northern Caucasus, but the development of agriculture in Russia during the next ten years promises to be very intensive, and *Bradyporus* will, undoubtedly, become extinct in many more localities before long.

The Balcanian and the Anatolian species of the genus inhabit mainly the stony and semidesert areas and this ensures, that they may be preserved for a longer time, but still it is necessary that these largest and most peculiar representatives of European *Teettigoniidae* should be fully studied as soon as possible. Still more desirable is a thorough study of the Russian species, since the data communicated in the present paper are far from exhausting the problems connected with this insect, which Prof. Lindeman 25 years ago called «the most interesting representative of our Russian fauna and deserving careful studies».

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Explanation of Plate 1.

Fig. 1.—*Bradyporus multituberculatus* F. W., ♂, singing on *Rhamnus pallasii.*
Fig. 2.—Copulating pair of *Br. multituberculatus* F. W.

Fig. 1.

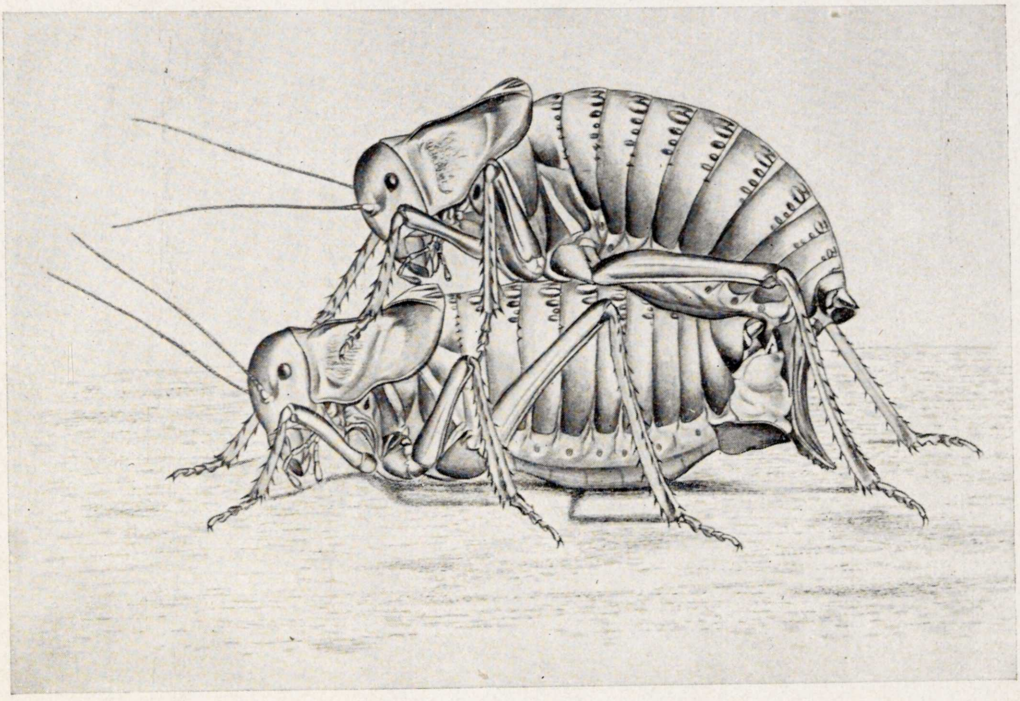

Fig. 2. A. A. Bayukova, del.

B. Th. Boldyrev: Biological Studies on *Bradyporus multituberculatus* F. W.